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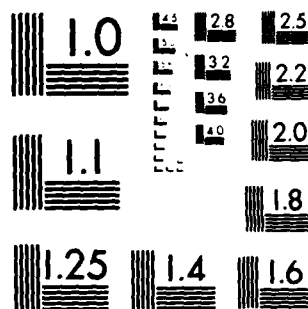
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7 disparity selective neurons that are optimally stimulated at the horopter tend to be more binocular than cells selective for nonzero disparities. Second, cortical cells with large receptive fields tend to be more binocular and can maintain larger disparities than small-field cells. Third, low levels of uncorrelated activity allow changes in ocular dominance that accentuate any ocular dominance organization present prior to visual experience. The model also readily accounts for the loss of binocularity caused by monocular deprivation, alternating occlusion, and strabismus.



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Correlation of Afferent Activity  
and Binocular Receptive Field Properties\*

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## Abstract

A theoretical model of synaptic plasticity is used to examine the importance of the correlation of left eye and right eye afferent activities for the development of binocular receptive field properties in visual cortex. Generally, cortical cells that receive less binocularly correlated activity become less binocular. We argue that larger disparity decreases correlation and larger receptive field size increases correlation. Therefore, the consequences of normal uncorrelated activity are: first, disparity selective neurons that are optimally stimulated at the horopter tend to be more binocular than cells selective for nonzero disparities. Second, cortical cells with large receptive fields tend to be more binocular and can maintain larger disparities than small - field cells. Third, low levels of uncorrelated activity allow changes in ocular dominance that accentuate any ocular dominance organization present prior to visual experience. The model also readily accounts for the loss of binocularity caused by monocular deprivation, alternating occlusion, and strabismus.

The receptive fields of neurons in kitten striate cortex are usually characterized by their size and response properties such as orientation selectivity, direction selectivity, disparity selectivity, and binocularity. Most cells can be activated by stimulation of either eye (Hubel and Wiesel, 1962) and therefore have one receptive field on the left retina and another on the right retina. If a stimulus strikes both left and right receptive fields, a cortical neuron receives correlated trains of impulses from the two eyes. Although some cells may innately respond only to very specific types of stimuli, prior to visual experience a large number of cortical neurons are broadly tuned or unselective for both stimulus orientation and disparity (Hubel and Wiesel, 1963; Barlow and Pettigrew, 1971; Pettigrew, 1974; Blakemore and Van Sluyters, 1975; Buisseret and Imbert, 1976; Sherk and Stryker, 1976). These immature traits are refined during the critical period for synaptic plasticity which lasts for approximately the first three months of life (Hubel and Wiesel, 1970).

We have used a theoretical model of plasticity in the developing visual system to study the maturation of receptive field properties. In particular, we have examined the conditions under which binocular cells in normal animals receive partially uncorrelated activity (the trains of impulses from the two eyes being partially uncorrelated) and how this activity affects development. This is an extension of theoretical (Bienenstock et al., 1982; Cooper et al., 1979) and experimental (see Movshon and Van Sluyters, 1981 for review) studies which have demonstrated that correlated binocular activity is of critical importance for the maintenance of binocularity in cortical neurons. We find that the relatively small amount of uncorrelated binocular activity that occurs in normal kittens can be a significant determinant of receptive field properties. We claim that the amount of binocular correlated activity that reaches a cortical neuron in a young kitten is determined largely by the distance from the horopter at which the left and right receptive fields are in

register (the cell's disparity) and by the receptive field size. Because the amount of binocular correlation affects a cell's ocular dominance, relationships develop between the cell's disparity, binocularity, and receptive field size. The consequences of the theory are that: first, cells whose fields are initially in register at the horopter (low disparity) remain more binocular than cells with larger disparities. Second, binocularity and maximum disparity increase with receptive field size. Third, any ocular dominance organization present prior to visual experience is accentuated. The principal virtue of the theoretical analysis is that seemingly unrelated experimental observations can be unified because they are different manifestations of the same mechanism of plasticity. This allows receptive field development to be viewed as a single process instead of a conglomeration of changes in many individual response properties. The model also readily predicts the results that would be obtained by rearing animals in abnormal environments which affect binocular correlation. A brief account of this work has already been given (Paradiso, 1983).

#### Assumptions

In the mathematical model we may isolate the effects of various parameters on the overall development of visual cortex but we must specify the innate selectivity of cortical neurons and any changes in connectivity caused by visual experience. Therefore, the following assumptions are made -

- 1) Innately, a large number of cells in striate cortex are broadly tuned or unselective for both stimulus orientation and disparity (Barlow and Pettigrew 1971, Pettigrew 1974, Blakemore and Van Sluyters 1975, Buisseret and Imbert 1976). The wide range of binocular facilitation observed in kittens' cells (Pettigrew, 1974) and the much narrower range seen in adults (Pettigrew et al., 1968) suggests that at birth the inhibitory zones in



receptive fields are relatively undeveloped.

2) Prior to visual experience there is a considerable overlap of the thalamic afferents subserving the two eyes and during the critical period there is a 'sharpening' of ocular dominance columns (LeVay et al. 1978).

3) Each neuron in the visual pathway can be characterized by its firing frequency (Figure 1). Although we treat these frequencies as instantaneous variables they may be considered to be moving time averages of the actual instantaneous rates where the length of averaging is of the order of the magnitude of the membrane time constant.

4) Visual experience can alter the response properties of cortical neurons through changes in synaptic efficacy. Evidence from both invertebrate (Kandel and Schwartz, 1982) and vertebrate (Levy and Steward, 1979) preparations supports this notion.

5) Changes in synaptic strength depend on the correlation of the firing of presynaptic and postsynaptic neurons. Hebb (1949) proposed that synapses strengthen when presynaptic and postsynaptic cells are simultaneously active. We employ a Hebbian form of synaptic modification which is described by Bienenstock et al. (1982) and summarized in the appendix. Rauschecker and Singer (1979, 1981) and Cynader and Mitchell (1977) have performed experiments which support the hypothesis that the correlation of cell activities governs changes in synaptic efficacy.

To describe the ocular dominance of cortical neurons we introduce a quantitative index -

$$\text{ocular dominance} = \frac{c_r}{c_l + c_r}$$

where  $c_l$  and  $c_r$  are the maximum response frequencies of the cortical cell obtained by monocular stimulation of the left or right eye with the optimal pattern. A value of 0.0 means the cell is left eye monocular and a value of

1.0 indicates a right eye monocular cell. We have purposefully refrained from classifying the ocular dominance on a scale of 1 - 7 or 1 - 5 to avoid any misleading resemblance to physiological ocular dominance classifications. Macy et al. (1982) report that the relationship between subjective and objective measures of ocular dominance is not always straightforward.

### Results

The fundamental result obtained by introducing uncorrelated binocular activity into the theory described by Bienenstock et al. (1982) is that the amount of correlated activity a cell receives determines its final state of ocular dominance. Figure 3 shows the effect of varying the percentage of correlated binocular activity which reaches a single postsynaptic cortical cell. The cell receives 19 afferents from each eye (figure 2) and 'views' oriented visual patterns selected randomly from an environment of 25 patterns (see Appendix for description of the pattern environment). The synapses from the 38 afferents were initialized such that all patterns produced an equal postsynaptic response in the cortical cell and neither eye was dominant. The initial response properties are illustrated in figure 3A where the vertical axis indicates the cell response to each of the pattern orientations in one 180° cycle shown on the horizontal axis. The final tuned states in figures 3B,C,D were each obtained by presenting the cortical cell with exactly the same sequence of 40,000 patterns. The three final states differ only in that they were obtained by letting the cell see different degrees of uncorrelated activity. The state in figure 3B resulted from presenting the left and right 'eyes' with the same pattern 10 % of the time (10 % correlated activity) and with different randomly chosen patterns 90 % of the time. Similarly in figures 3C and 3D the cell received 60 % and 90 % correlated activity, respectively. The final states illustrate that the eventual ocular dominance

of the cell is related to the degree of correlation in the binocular activity. With only 10 % correlation the cell quickly became monocular and orientation selective (ocular dominance index = 0.06). With 90 % correlation the cell was orientation selective in both eyes and the response remained completely binocular (ocular dominance = 0.48). The intermediate case with 60 % correlation demonstrates orientation selectivity comparable to the other cases and a response dominated by the left eye, though not monocular (ocular dominance = 0.21). Several conclusions can be drawn from these computer simulations: first, uncorrelated activity disrupts binocularity and any rearing condition which decreases correlation will produce more monocular cells. Second, even in normal rearing conditions, cells that for any reason receive significant uncorrelated activity will tend to be relatively monocular. Third, orientation selectivity can develop normally irrespective of the correlation of the afferent activity. As long as there is substantial correlation in the activity, the optimal orientations are the same in both eyes regardless of the initial state. Fourth, the effects of the uncorrelated activity become evident during the same period of time in which orientation selectivity develops. Once a cell has become orientation selective, it will be less likely to receive uncorrelated activity because of the presence of well defined inhibitory zones in the receptive fields. Finally, mention should be made of one conclusion which cannot be drawn from these results - the exact percentages of correlation and their effects on binocularity are only useful in a relative sense. The rates of the shifts in ocular dominance depend on the particular numerical values of parameters in the equations for synaptic plasticity (see Appendix). Mathematical analysis indicates that the rate of shift away from perfect binocularity is, on the average, a linear function of the percentage of uncorrelated activity and of the degree of monocularity but a nonlinear function of other parameters such as the normalization of the input patterns (Paradiso, 1984). At any rate, the parameter values chosen in the model affect largely the quantitative aspects

of the results and not the qualitative relationships which are predicted.

The results of computer simulations suggest that the correlation of afferent activities from left and right eyes is crucial for the preservation of binocularity irrespective of the particular visual environment. We have simulated strabismus, monocular deprivation, and alternating occlusion (also see Bienenstock et al., 1982): for strabismus the 'eyes' were shown different, randomly chosen patterns. To simulate monocular deprivation the left eye was shown patterns selected randomly from an environment of 25 patterns while cortical afferents from the right eye fired randomly and independently of each other to simulate spontaneous activity. This procedure of presenting patterned stimuli to one eye and noise to the other was also employed to simulate alternating occlusion: after every presentation of 4000 patterns the eyes receiving noise and patterned stimuli were reversed until the total 40,000 patterns had been shown. The three abnormal rearing conditions produce little binocular correlation because the left eye and right eye afferents carry different, unrelated patterns of activity. In each case cortical cells become monocular and orientation selective yielding response curves the same as the low correlation case shown in figure 3B. The key variable is the amount of binocular correlation. Experimental (Hubel and Wiesel, 1965; Wiesel and Hubel, 1963) and theoretical (Bienenstock et al., 1982; Cooper et al., 1979) studies have shown that in these extreme cases of low correlation rearing, almost all binocularity is lost.

The highly evolved visual systems of macaque monkeys and cats both are organized to some degree into ocular dominance 'columns' - regions of visual cortex where cells have visual responses dominated by one eye (Hubel and Wiesel, 1965; 1972). These regions are arranged into anatomically demonstrable patches or stripes of ocular dominance, particularly in laminae heavily innervated by thalamic afferents (Shatz et al., 1977; Hubel and Wiesel, 1972). Especially in the cat, there is a considerable sharpening of these ocular dominance columns during the early weeks of visual experience

(LeVay et al., 1978).

We have also applied the theory to the development of an array of 625 independent cortical cells to see what effect low levels of uncorrelated activity have on the ocular dominance columns. The available experimental evidence suggests that genetic factors may establish a weak periodic variation in ocular dominance across cortex (see Movshon and Van Sluyters, 1981 for review). Therefore, the 625 cells were initialized so that all neurons were highly binocular but there was a rough alternation of zones weakly preferring the left or right eye - figure 4A illustrates the initial state of the array of cells. Each neuron is represented by its index of ocular dominance equal to  $c_r / c_l + c_r$ . All cells in the initial state have values of this index between 0.45 and 0.55 - that is, all cells are highly binocular because of the presumed overlap of contralateral and ipsilateral fibers. The synapses to each neuron were initialized so that there was no orientation selectivity but the results would be the same if some cells were orientation selective. The top left frame in figure 4 shows the initial variation in the ocular dominance index along a diagonal 'penetration' through the array. The amount of correlated activity which reached each neuron was assigned at random. For example, one cell might receive correlated activity 80 % of the time and its neighbor might receive 70 % or 90 % correlated activity. Figures 4B and 4C show the array of cells after presentation of 40,000 patterns; in the simulation for figure 4B each cell received an amount of correlated activity chosen randomly (normal distribution) with mean = 80 % and standard deviation = 10 % whereas in figure 4C they were chosen with mean = 60 % and standard deviation = 10 %. In both cases the values of the ocular dominance index indicate the 'sharpening' of the regions of left- and right- eye dominance (values shifted toward 0.0 or 1.0). However, with less correlated activity (figure 4B) there is much less binocularity than the case with high correlation (figure 4C). As a rough measure of the development of regions of

ocular dominance, cells with an ocular dominance index of less than 0.45 (left eye dominant) have been shaded. Clearly this shading is not equivalent to the columns demonstrated by autoradiographic techniques (eg. Shatz et al., 1977) because in our figures all cells are binocular to some extent. However, the results suggest that a form of ocular competition in normal animals can significantly enhance any innate organization - it is only necessary that a rough outline of the ocular dominance structure be layed out prior to visual experience. This accentuation is particularly pronounced because, as mathematical analysis shows (Paradiso, 1984), binocularity is lost quickest in those cells initially farthest from perfect binocularity (ie. ocular dominance = 0.5). The fluctuations in ocular dominance along diagonal 'penetrations' are again illustrated on the left where shading represents left eye dominance. Because the cortical cells develop independently in this model, occasionally there are quite binocular cells located in the midst of ocular dominance columns and monocular cells located near the borders of the columns. However, it is found that with the addition of intracortical connections between neurons, neighboring cells are more likely to have the same ocular dominance (Scofield and Cooper, to be published) - this produces smoother variations in ocular dominance across the columns.

### Discussion

The results of this theoretical study show that, in a simple learning model, the degree of correlation between inputs from the two eyes impinging on a visual cortical neuron will have a significant effect on its binocularity. These findings are consistent with extensive experimental evidence that conditions which disrupt the correlation between afferent input from the two eyes lead to a drastic reduction in binocularity. The following discussion will focus on a further implication of this work. Neurons of visual cortex

normally have receptive fields in each eye and a well - focussed image is more likely to lie simultaneously in both of these fields if they are large and have little or no disparity in the fixation plane. Thus, from our results we would expect binocularity in cortical cells to be positively correlated with receptive field size and negatively correlated with receptive field disparity.

In animals with binocular vision the striate cortex in each hemisphere contains two topographic maps of visual space - one for each eye. The innate 'wiring' results in some cortical cells with precisely corresponding receptive fields in the two retinae and other cells which have mismatched receptive fields to some extent. This fact was used by Joshua and Bishop (1970) to define a horopter for the adult cat as the surface in space on which the maximum number of cells have their left and right receptive fields in register during fixation. When the animal fixates, the left and right receptive fields for different cells will be in register at different distances - some cortical cells will have receptive fields in register in front of the horopter (figure 5A), some will be in register at the horopter (figure 5B), and others will be in register behind the horopter (figure 5C).

The distance away from the horopter at which the receptive fields are in register is related to the amount of correlated activity the cortical cell will receive. When a cat fixates for near vision there are lens movements (accommodation) which bring near objects into focus on the retina (Vakkur and Bishop, 1963; Hughes, 1977). Estimates of the range of accommodation in cats have ranged from 3 - 11 diopters (see Hughes, 1977 for review). For a given diameter of the pupil there is a depth of field or range of distances in which objects can move about the horopter and still remain in focus. For example, for a fixation distance of 1 m, a 4 mm pupil the depth of field extends from 0.97 m to 1.03 m (Moseley, 1970). Beyond this range the eye must either change the accommodation or see a blurred image. As a result, when the animal fixates, the contrast on the retina decreases as a stimulus moves away from the horopter. Furthermore, it has been reported that the cortical evoked

potential (Campbell et al., 1973) and single unit firing frequencies (Ikeda and Wright, 1974) are linearly related to the logarithm of the contrast of sinusoidal gratings. This suggests that as objects move away from the horopter the cortical response decreases as the retinal contrast decreases.

Therefore, the limited depth of field is an important determinant of the type of stimuli that will excite the cortical cells whose receptive fields are shown in figure 5. In figure 5B the receptive fields are in register at the horopter and by definition, an object at this distance will be in focus on both retinae. The cortical cell possessing these receptive fields will receive mainly correlated binocular activity and a small amount of weaker uncorrelated activity stimulated by objects away from the horopter. Conversely, in figures 5A and 5C the high contrast, in focus stimuli at the horopter are more likely to produce uncorrelated activity whereas the 'best' binocular stimulus located where the receptive fields maximally overlap will produce little activity because it is blurred on the retinae. These types of cortical cells receive considerably more uncorrelated activity than those with fields as in figure 5B.

Using this argument to reinterpret the results presented earlier suggests that cells 'looking at the horopter' will in general be more binocular than those looking behind or in front of the horopter because they receive more correlated, in-focus stimulation when the animal fixates. There are several pieces of experimental data from cat and macaque monkey studies which indicate that such a relationship exists. Both of these species are known to possess good stereopsis (Fox and Blake, 1971; Packwood and Gordon, 1975; Bough, 1970). Early studies of the binocular responses of cortical cells in cats revealed that the disparity tuning curves of some cells were asymmetrical in shape (Pettigrew et al., 1968). In other words, the receptive fields were organized such that the response might gradually decrease as the stimulus moved further away than the optimal distance but would quickly stop if the stimulus moved nearer. These asymmetrically responsive cells were commonly in the more



extreme ocular dominance groups and it was suggested that they might signal whether a stimulus is behind or in front of the fixation point. This supposition was given credence when distance sensitivity was studied in visual cortex using macaque monkeys trained to fixate on a screen (Poggio and Fischer, 1977). Cells selective for distance (84 % of those sampled) were separated into several classes - in the first group, cells were tuned for a depth about the horopter and were found to receive a balanced binocular input. The other classes were tuned for near stimuli (relative to the horopter), far stimuli, or inhibited by stimuli at the horopter. These cells with disparity received unbalanced binocular input. The use of unanaesthetized fixating animals makes this strong evidence that cells selective for near or far distances are less binocular than those selective near the horopter. Additional studies performed using anaesthetized and paralyzed cats (Fischer and Kruger, 1979; Ferster, 1981) also support this idea. Although the animals could not fixate, they were found to have the same types of disparity selective neurons that had been found in the monkey. Again, those cells selective for zero disparity were more binocular than cells tuned for larger disparities.

The other major factor which affects the correlation of afferent activity and the binocularity of a cortical cell is the receptive field size. For instance, figure 6 pictures the receptive fields of two cortical cells; in one case the left and right receptive fields are  $50^\circ$  across and in the other case they are  $10^\circ$  across. Measurement at the horopter of the angle between the left and right field centers shows that both cells have the same disparity. However, the receptive fields for the large - field cell overlap at points much closer to the horopter (and within the depth of field) than those of the small - field cell. This implies that the large - field cell is more likely to receive high contrast binocular stimulation than the small - field cell. Consequently, the large - field cell will receive more correlated input and will remain more binocular. This result is consistent with experimental

observations that in all cortical laminae, cells with smaller receptive fields are less binocular (Leventhal and Hirsch, 1978). Furthermore, it has been reported that as receptive fields increase in size at higher eccentricities (Albus, 1975a) the binocularity of cortical neurons also increases (Albus, 1975b; Leventhal and Hirsch, 1980).

To summarize, it appears that larger disparities decrease binocularity and larger receptive fields increase binocularity. These two forces will interact to produce an observable result - one should find that maximum disparity increases with increasing field size. In other words, if there is a maximum degree of uncorrelated activity that a cell can receive without disrupting binocularity then large - field cortical cells can maintain larger disparities than small field cells. This has not been observed directly but it has been reported that the range of disparities increases with increasing horizontal eccentricity (Joshua and Bishop, 1970). This observation combined with the increase in receptive field size with eccentricity (Albus, 1975a) suggests that maximum disparity increases as receptive field size increases.

Joshua and Bishop (1970) proposed that the range of disparities found in the adult cat may underlie the feline equivalent of Panum's fusional area. Panum's area is the region behind and in front of the horopter in which objects can move without disrupting binocular single vision. If a stimulus moves outside this zone without commensurate eye movements double vision results. It has been known for some time that Panum's area in man has greater breadth at larger eccentricities (Ogle, 1950). That is, at higher eccentricities a stimulus can be located farther from the horopter without disrupting binocular single vision than at lower eccentricities. It is likely that the increased breadth of Panum's area at high eccentricities is caused by the increased range of disparities possessed by eccentric cells. The model is consistent with this notion and suggests that this phenomenon may be based on the increase in receptive field size with eccentricity which is determined by the retino - geniculo - cortical mapping.

In addition to the influence on receptive field maturation, uncorrelated activity may also have a global effect on ocular dominance columns. The results of computer simulations demonstrate that low levels of uncorrelated activity allow relatively small changes in ocular dominance which accentuate any ocular dominance organization which is innate. The sharp columns obtained in figure 4B are similar to those seen in layers in visual cortex which receive direct thalamic innervation (Hubel and Wiesel, 1972; Shatz and Stryker, 1978). The 'fuzzier' columns in figure 4C might be similar to the ocular dominance organization in layers not heavily innervated by lateral geniculate afferents where ramifications of intracortical neurons spread visual activity and produce higher degrees of correlation.

In general, any condition which decreases binocular correlation will alter the appearance of ocular dominance columns. In normal animals the ranges of receptive field size and disparity (and intracortical connections) establish the amounts of correlation and influence the normal columnar pattern. More distinct ocular dominance columns have been observed in strabismic kittens (Shatz et al., 1977) and there are changes in both size and definition of columns in monocularly deprived animals (Shatz et al., 1977; Shatz and Stryker, 1978); both of these abnormal rearing conditions disrupt binocular correlation. Presumably dark rearing also decreases the likelihood of binocular correlation but in that situation neither eye receives repeated patterns of stimulation that might allow it to suppress the other eye. In computer simulations dark reared cells remain binocular. The results of mathematical analysis and computer simulations of several abnormal rearing conditions have been presented in detail by Bienenstock et al., 1982. It is significant that the simple form of synaptic modification we have employed can explain, with relatively few prior assumptions, the development of precise receptive field properties in cortical neurons both under normal and abnormal rearing conditions.

## Appendix

### A Model of Synaptic Plasticity and Cortical Development

We summarize here a theory proposed for the development of feature selectivity in visual cortex (Bienenstock et al., 1982; Munro, 1983; Cooper et al., in press). Each neuron in the visual pathway is characterized by its firing frequency: the frequency of a cortical cell at time  $t$  is  $c(t)$  and the frequency of the  $j$ th thalamic afferent projecting to the cortical cell is  $d_j(t)$  (Figure 1). The postsynaptic response is assumed to be a simple linear function of the presynaptic activities -

$$c(t) = \sum_j m_j(t) d_j(t)$$

where  $m_j(t)$  indicates the strength of the synapse between the cortical cell and the  $j$ th afferent. Learning is manifested in the changes in the synaptic weights governed by the modification rule -

$$\dot{m}_j(t) = \phi(c(t), q(t)) d_j(t)$$

In words, the change in the strength of the  $j$ th synapse is equal to the product of the firing frequency of the  $j$ th afferent ( $d_j$ ) and a modification function  $\phi$ . This equation is similar to the learning rule proposed by D.O. Hebb (1949) to account for the results of classical conditioning experiments. According to Hebb's hypothesis the change in synaptic strength ( $\dot{m}$ ) might be simply the product of presynaptic and postsynaptic activities (ie.  $\dot{m}_j(t) = c(t)d_j(t)$ ). The introduction of the  $\phi$  function modifies Hebb's learning rule such that a wide variety of results from electrophysiological studies of visual cortex can be explained (Bienenstock et al., 1982). The value of  $\phi$  is a function of the spike

frequency of the postsynaptic cell ( $c(t)$ ) and  $q(t)$  which is a running time average of the postsynaptic activity:

$$q(t) = \exp(-\beta q_0 t) + \beta \int_0^t \exp(-\beta c(t') t') dt'$$

$$q(t) = \beta(c - q) \quad \beta > 0$$

A variety of modification functions  $\phi$  can be used as long as several conditions are satisfied -

$$\phi(c, q) > 0 \text{ for } c > \theta_m$$

$$\phi(c, q) < 0 \text{ for } c < \theta_m$$

$$\phi(0, q) = 0 \text{ for all } q.$$

The first two conditions provide that synapses strengthen ( $\phi > 0$  and  $\dot{m} > 0$ ) when the postsynaptic response ( $c$ ) is greater than a modification threshold ( $\theta_m$ ) and weaken ( $\phi < 0$  and  $\dot{m} < 0$ ) when the response is less than the modification threshold. The modification threshold is taken to be a function of the time averaged postsynaptic activity,  $\theta_m = (\text{constant}) (q^p)$  where  $p > 1$ . The third condition states that there is no synaptic change when the postsynaptic cell is quiescent. Synaptic modification functions which satisfy these requirements have been shown to produce binocular orientation selective cells (Bienenstock et al., 1982; Munro, 1983).

For the binocular simulations described in the Results the postsynaptic response has been generalized to include afferents from both eyes -

$$c(t) = \sum_j (m_{jL}(t) d_{jL}(t)) + \sum_j (m_{jR}(t) d_{jR}(t))$$

where  $m_{jL}(t)$  and  $m_{jR}(t)$  represent the synapses with afferents from the left and right eyes. The patterns of afferent activity from the two eyes ( $d_{jL}(t)$  and  $d_{jR}(t)$ ) may be correlated or uncorrelated. When we say a cell receives 80 % correlated activity we mean that 80 % of the time the eyes are shown the same pattern of afferent activity and 20 % of the time the eyes were shown different randomly chosen patterns.

The patterns of afferent activity  $d = (d_1, d_2, \dots, d_n)$  are randomly chosen variables uniformly distributed on a circularly symmetric closed one - parameter family of points in the space  $R^N$ . This theoretical environment is used both as input to the cortical neurons during development and as a test environment to construct a tuning curve. The patterns are analogous to the typical laboratory stimuli consisting of slits of light which differ only in one parameter - their orientation.

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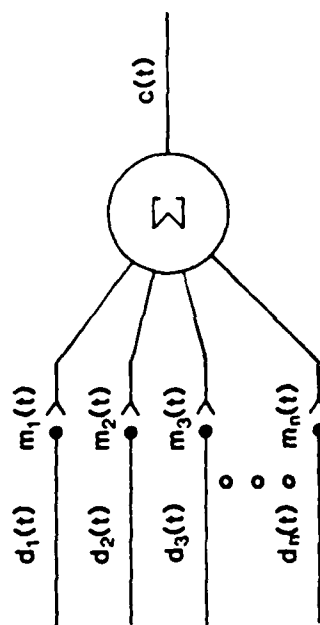


Figure 1

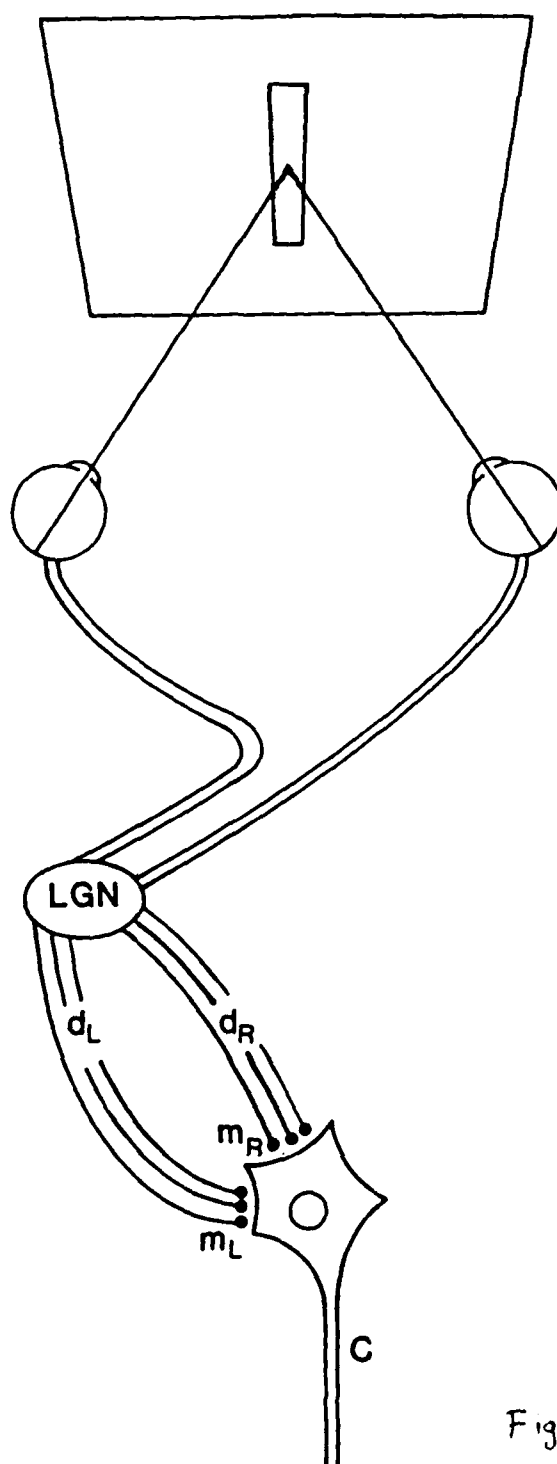


Figure 2

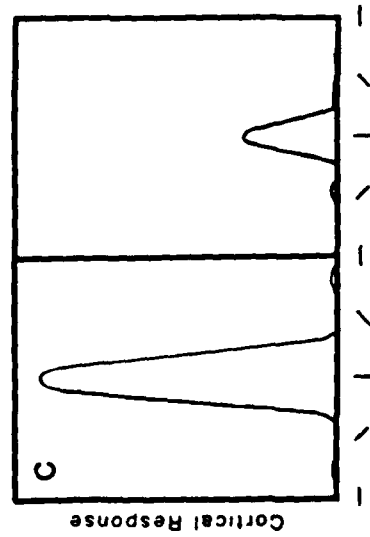
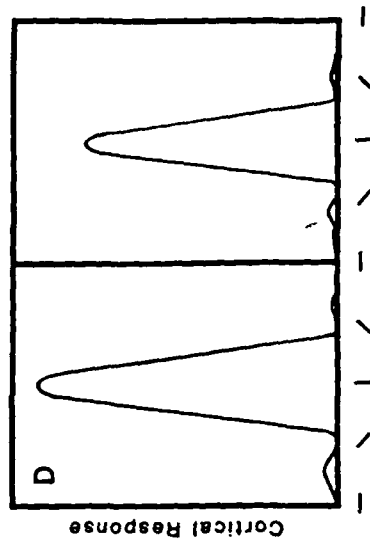
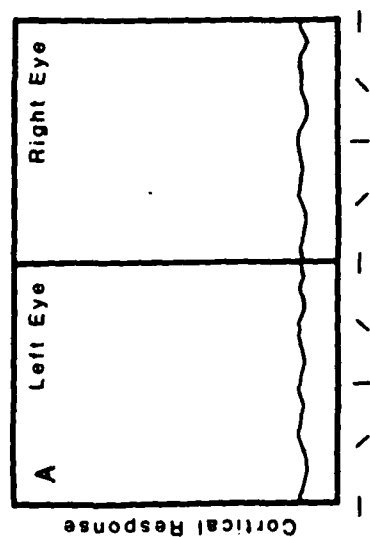
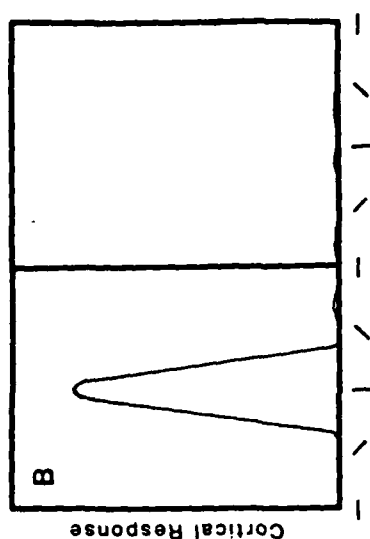


Figure 3

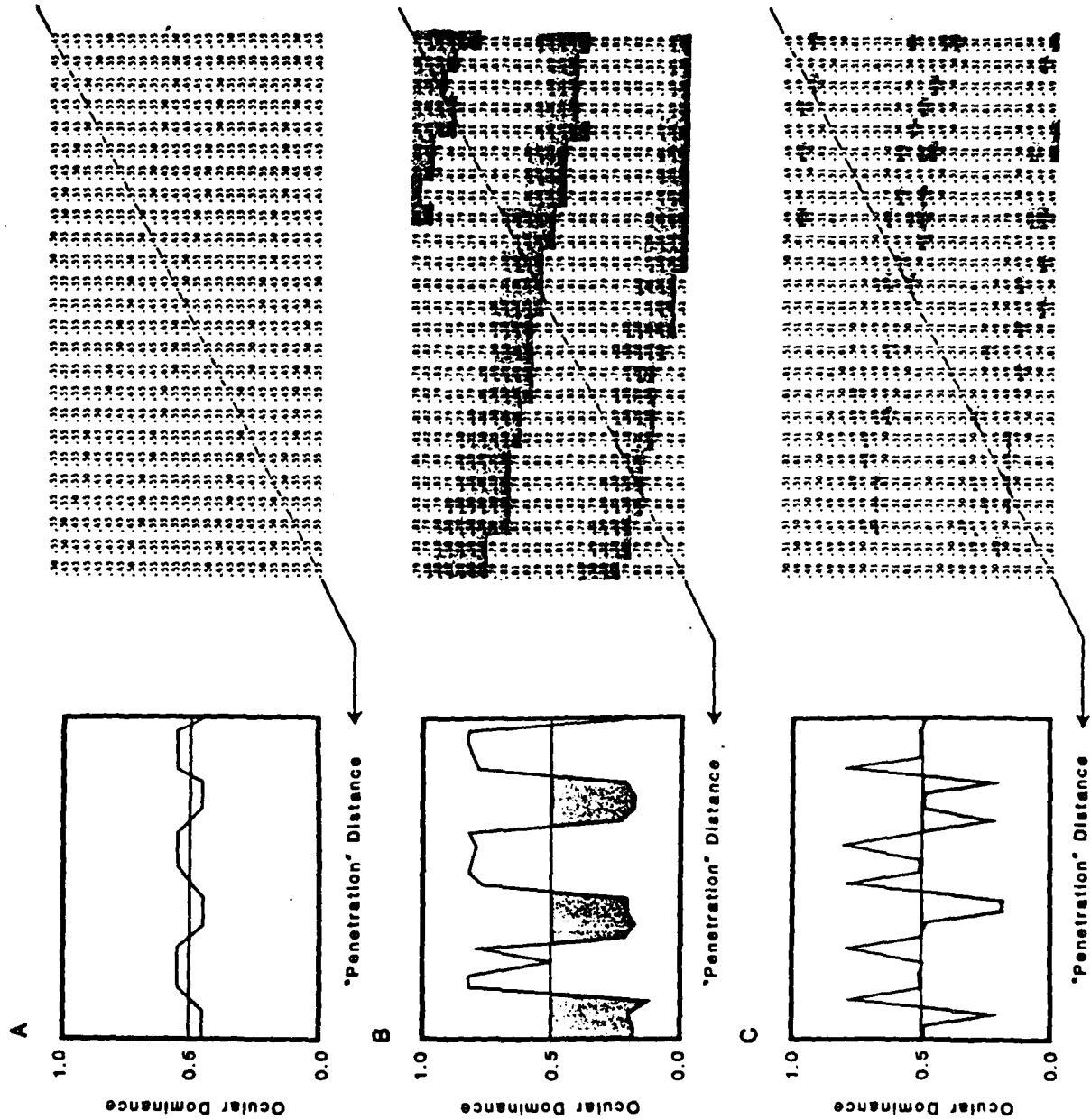


Figure 4



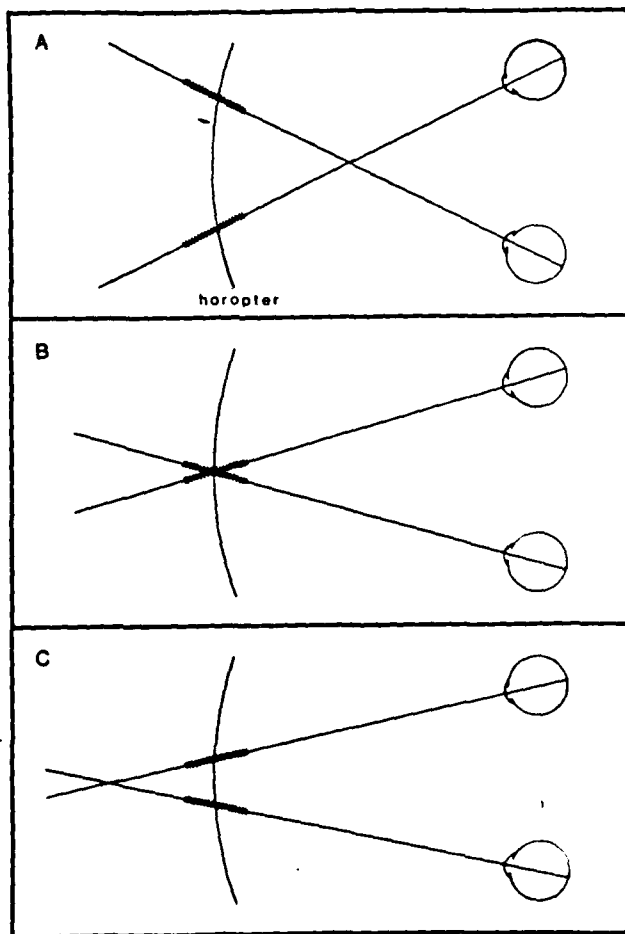


Figure 5

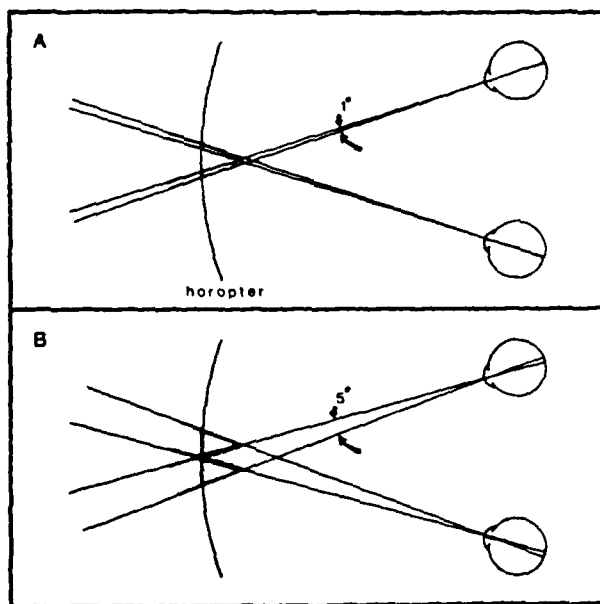


Figure 6

### Figure Captions

1. In the mathematical model of synaptic plasticity and learning each cell in the visual pathway is characterized by its firing frequency. The frequency of a cortical cell,  $c(t)$ , is a linear function of the  $n$  thalamic afferent firing rates,  $d(t)$ . The strength of the synapse between the cortical cell and the  $j$ th afferent is  $m_j(t)$ . Details of notation are described in the Appendix.
2. A single binocular cortical neuron receives 19 afferents from each eye. Left eye and right eye afferents in the optic radiation are represented by  $d_l$  and  $d_r$ . The eyes 'see' oriented patterns selected randomly from a circular environment of 25 patterns. Synapses in the lateral geniculate nucleus (LGN) are not considered modifiable.
3. The effect of binocular correlation on the ocular dominance of cortical cells. (A) is the binocular unselective initial state before visual experience. The vertical axis indicates the cortical cell response (firing frequency) to the 25 patterns in a  $180^\circ$  cycle indicated on the horizontal axis. (B), (C), and (D) are final states obtained after presentation of 40,000 patterns. In (B) there was 10 % correlated activity and ocular dominance = 0.06. In (C) there was 60 % correlated activity and ocular dominance = 0.21. In (D) there was 90 % correlated activity and ocular dominance = 0.48. Higher correlation yields more binocular final states.
4. Uncorrelated binocular activity accentuates ocular dominance columns. The initial states of 625 cortical cells are highly binocular (A) - the ocular dominance index for each cell is between 0.45 and 0.55. (B) and (C) are final states after presentation of 40,000 patterns to each

cell. The cells in (B) were randomly assigned to receive some amount of correlated activity (normal distribution, mean = 80 %, standard deviation = 10 %). The percentage of correlation for each cell in (C) was also assigned randomly but mean = 60 % and standard deviation = 10 %. The left side frames show the variations in ocular dominance along diagonal 'penetrations'. Left eye dominant cells with an ocular dominance index less than 0.45 have been shaded. Lower correlation yields more distinct ocular dominance columns.

5. Left eye and right eye receptive fields may be in register in front of the horopter (A), at the horopter (B), or behind it (C). In (B) the high contrast stimuli at the horopter (cross hatching indicates the depth of field) activate both left and right receptive fields. In (A) and (C) the high contrast stimuli within the depth of field can produce relatively more monocular activity.
6. Receptive fields of two cortical cells with the same disparity. The large - field cell (B) is more likely to receive high contrast binocular activity than the small - field cell (A) because its left and right receptive fields overlap within the depth of field (cross hatched).

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